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On the dynamics of predation risk perception for a vigilant forager.

Etienne Sirot[1] and Olivier Pays[2]

1 - Laboratoire Ecobio, UMR CNRS 6553,

Université de Rennes 1, Campus de Beaulieu, 35042 Rennes, France.

2 - LEESA, Groupe Ecologie et Conservation,

Université d'Angers, Campus Belle Beille, 2 Bd Lavoisier, 49045 Angers, France.

Correspondence : Etienne Sirot, LEMEL, Université de Bretagne Sud, Campus de Tohannic, BP 573, 56017 Vannes, France.

E-mail : sirot@univ-ubs.fr, Phone : 02 97 01 71 49, Fax : 02 97 68 16 39.

ABSTRACT

Foraging animals often raise their head to scan for predators. Scanning intervals have variable durations, and occur more or less frequently, depending on ecological conditions. Our study relies on the assumption that temporal patterns of vigilance depend on the speed with which information concerning the likelihood of a predator's presence in the neighbourhood is gathered when an animal is vigilant, and lost when it is not. Using an analytical model, we study how the perceived level of risk progressively decreases, when the individual is vigilant and detects no predator, then increases again, when it lowers its head to feed, thereby losing most of its detection abilities. The speed of these variations is affected by the likelihood of the presence of a predator in the whole environment, by the mobility of this predator, and by the detection capacities of the prey. We show how, combined with the range of risk levels tolerated by this animal, this dynamics determines the frequency and the duration of its scanning intervals. The dynamics of risk perception can also explain particular behavioural patterns, such as the progressive decrease of vigilance that may occur after the arrival into a novel environment, and the central tendency in the distribution of interscan durations reported by many studies. Next, we use the model to compute optimal vigilance strategies, taking into account the trade-off between feeding and limiting exposure to predators. The model predicts that a forager will scan more often, and for longer periods, when the likelihood a predator's presence in the surrounding environment is increased. A similar response is expected when the mobility of the predator is increased. By contrast, when the detection capacities of the prey are reduced, it will increase its vigilance by scanning for longer periods, but scanning intervals will be separated by longer interscans.

Keywords : anti-predatory behaviour, information, predation, risk, vigilance

INTRODUCTION

Time-sharing between anti-predatory vigilance and other activities, such as foraging, reproduction, or sleep, implies that animals have to trade some component of fitness (e.g. energy gain through feeding) for better security against predators (Elgar, 1989; Quenette, 1990). This trade-off has been studied by mathematical models that derived optimal or evolutionarily stable vigilance strategies as a function of ecological conditions (e.g. Pulliam et al., 1982; McNamara and Houston, 1992). The assumption of vigilance models is that individuals with high vigilance levels have more chance of detecting an approaching predator, hence more chance of escaping when under an attack. The level of vigilance is represented by a behavioural variable; namely, the scanning rate (e.g. Pulliam, 1973; Pulliam et al., 1982; Lima 1987; Rodriguez-Gironés and Vàsquez, 2002), or the proportion of time spent vigilant (e.g. Packer and Abrams, 1990; McNamara and Houston, 1992; Sirot, 2006).

Concurrently, temporal patterns of vigilance have been studied over a wide range of animal taxa, making the topic of anti-predatory vigilance a particularly fruitful example of joint development between theoretical and field work (Bednekoff and Lima, 1998). Field studies do indeed report that the proportion of time dedicated to vigilance varies with ecological conditions, but, moreover, that the duration of both scanning intervals and non vigilant intervals (interscans) may be affected by these conditions (e.g. Metcalfe, 1984; Whittingham et al., 2004; Pays et al., 2007). Measuring scans and interscans allows to calculate the proportion of time dedicated to vigilance, but also conveys more precise information, as different scanning rates may lead to the same proportion of time spent vigilant (e.g. Pöysä, 1994; Pays et al., 2007). A relevant question is thus to ask, not only what proportion of time should be allocated to vigilance, but also how total vigilance time should be apportioned among consecutive scans. This question is particularly important because predatory attacks are very sudden events, and the exact posture of the individual at the onset

of an attack may determine its chance of escape (Hilton et al., 1999). This is probably the reason why animals obey short-term decision rules that dictate the precise moments of head raising and lowering, as a response to immediate conditions (Bekoff, 1995; Pays et al., 2009).

In the present study, we use a behavioural model to study the alternation of scanning and interscan intervals for an isolated forager on a food patch. The model addresses the following questions: (1) how long should a forager that does not spot any predator stay vigilant before resuming food search? and (2) how long should it feed after resumption, before switching back to vigilance?

Our study relies on the assumption that the behaviour of the animal is dictated by its instantaneous perception of predation risk, which fluctuates as a function of its activity. In the first part of the article, we describe the dynamics of risk perception over a foraging period during which no detection occurs, successively considering what happens during feeding and scanning intervals. In the second part, we consider the trade-off between feeding and limiting exposure to predators, and derive optimal vigilance strategies.

THE MODEL

The model considers an isolated forager on a food patch, which shares its time between feeding and vigilance, considered as two mutually exclusive activities. The duration of the whole foraging process, T, is fixed. Feeding allows the individual to increase its level of energy reserves, while scanning is used to detect a potential predator. The forager's perception of risk at time t, $\mu(t)$, corresponds to the estimated probability of the predator's presence in the neighbourhood (i.e. within detection range).

P_0, initially assumed to be a constant, denotes the probability of the predator's presence in the whole environment, which encompasses both the neighbourhood of the forager and the surrounding places, which are not observable by the forager, but from which the predator may

arrive. Parameters s and S denote the areas of the forager's neighbourhood, and of the whole environment, respectively. The initial estimated probability of the predator's presence in the neighbourhood, when the forager arrives on the patch and has not yet had the opportunity to scan, is : $\mu_0 = P_0 \times s/S$. The level of risk that prevails in the forager's neighbourhood may nevertheless change with time, because the predator, if present, may move. During a small time interval dt, the predator moves with probability mdt, where m is a measure of its mobility. When moving, the predator arrives in the neighbourhood of the forager with probability s/S.

Interval $[\mu_1,\mu_2]$ corresponds to the range of risk levels tolerated by the animal. This means that the forager switches from vigilance to feeding when its perception of risk $\mu(t)$ reaches threshold μ_1 during a scan, and from feeding to vigilance when $\mu(t)$ reaches threshold μ_2 during an interscan.

We first determine the fluctuations of predation risk perception during successive scans and interscans, when no detection occurs. Then, we consider the trade-off between searching for food and scanning for the predator, and compute optimal vigilance strategies.

Variations of predation risk estimation during interscans

Here, we consider what happens when the forager keeps its head at ground level to feed, after a vigilant period. When the animal begins to feed, its estimation of predation risk is μ_1. Thereafter, due to its incapacity to track changes in the environment, its estimated level of risk changes, as a function of the predator's tendency to move and approach close by. t denotes the time elapsed since the animal began feeding, and $\mu_f(t,\mu_1)$ is its estimation of predation risk at time t. The initial condition is : $\mu_f(0,\mu_1) = \mu_1$.

$\mu_f(t+dt,\mu_1)$ estimates the probability of the predator's presence in the neighbourhood of the forager at time t+dt. Following the rules for predator movement described above, three

different reasons may explain this presence. First, the predator may already be present at time t, and be immobile during interval dt. This happens with probability $\mu_f(t,\mu_1) \times (1 - mdt)$. Second, the predator may already be present, move, and arrive again in the forager's neighbourhood. This happens with probability $\mu_f(t,\mu_1) \times mdt \times s/S$. Third, the predator may initially be present in another part of the environment, and move into this neighbourhood. This event occurs with probability $(P_0 - \mu_f(t,\mu_1)) \times mdt \times s/S$. Thus, we finally have :

$$\mu_f(t+dt,\mu_1) = \mu_f(t,\mu_1) \times (1 - mdt) + \mu_f(t,\mu_1) \times mdt \times s/S + (P_0 - \mu_f(t,\mu_1)) \times mdt \times s/S \quad (1).$$

or : $$\mu_f(t+dt,\mu_1) = \mu_f(t,\mu_1) \times (1 - mdt) + \mu_0 \times mdt, \text{ as } \mu_0 = P_0 \times s/S \quad (2).$$

This leads to the differential equation : $d\mu_f/dt \times 1/(\mu_f - \mu_0) = -m$ (3).

The solution of Eq. (3) is : $\mu_f(t,\mu_1) = (\mu_1 - \mu_0) \times \exp(-mxt) + \mu_0$ (4).

Eq. (4) describes the dynamics of predation risk perception when the animal feeds. It shows how the level of risk perceived progressively rises, tending towards its basic level μ_0, when the animal keeps its head down. Since the animal switches back to vigilance when the level of risk perceived reaches threshold μ_2, we have : $\mu_2 = \mu_f(t_f,\mu_1)$ (5), where t_f denotes the duration of the current feeding interval.

Information gathering during vigilance

Here we study how the level of risk perceived changes over one scanning interval, still under the assumption that no detection occurs. $\mu_v(t,\mu_2)$ is the estimation of predation risk at time t, the time elapsed since the individual started being vigilant. μ_2 is the perceived level of risk at the beginning of the vigilant period, so we have : $\mu_v(0,\mu_2) = \mu_2$. When considering predator movements only, predation risk follows the same dynamics as during interscans. Thus, the estimated probability of the predator's presence at time t+dt is given by : $\mu_v(t,\mu_2) \times (1 - mdt) + \mu_0 \times mdt$ (see Eq. (2)). However, the level of risk perceived by the forager at time t+dt is also

149 influenced by the fact that it did not detect the predator during interval dt. We must then
150 compute the probability of the predator's presence, conditional on the absence of a detection.
151 Parameter D, which measures the detection abilities of the forager, is the per time unit
152 probability of detection when a predator is present. Thus, the predator, when present, is
153 detected during small interval dt with probability Ddt, and remains undetected with
154 probability 1 - Ddt. When the predator is not present, the absence of detection occurs with
155 probability 1. Hence we get, using Bayes' formula :

156 $$\mu_v(t+dt,\mu_2) = \frac{(\mu_v(t,\mu_2)\times(1-mdt)+\mu_0\times mdt)\times(1-Ddt)}{(\mu_v(t,\mu_2)\times(1-mdt)+\mu_0\times mdt)\times(1-Ddt)+(1-(\mu_v(t,\mu_2)\times(1-mdt)+\mu_0\times mdt))\times 1}$$

157 (6).

158 Eq. (6) is built under the hypothesis that detection prevails over movements, that is, assuming
159 that the predator has the same chance of being detected if it moves to or from the forager's
160 neighbourhood during interval dt as if it had spent the whole interval within this
161 neighbourhood. This approximation, which concerns only rare events, was made to insure
162 coherence with the dynamics of risk perception during interscans, where detection ability is
163 cancelled (when D = 0, Eq. (6) collapses to Eq. (2)). Re-arranging Eq. (6) leads to the
164 following differential equation : $d\mu_v/dt \times 1/(\mu_v^2\times D - \mu_v\times(m+D) + \mu_0\times m) = 1$ (7).

165 The solution of Eq. (7) is : $$\mu_v(t,\mu_2) = \frac{a + b\times c\times\exp(-(b-a)\times D\times t)}{1 + c\times\exp(-(b-a)\times D\times t)}$$ (8),

166 where $a = \frac{(m+D) - \sqrt{((m+D)^2 - 4\times\mu_0\times m\times D)}}{2\times D}$, $b = \frac{(m+D) + \sqrt{((m+D)^2 - 4\times\mu_0\times m\times D)}}{2\times D}$, and

167 $c = \left|\frac{\mu_2 - a}{\mu_2 - b}\right|$. Eq. (8) shows how the level of risk perceived progressively decreases when the
168 forager is vigilant and does not detect the predator. The forager switches back to feeding
169 when the level of risk perceived reaches threshold μ_1, so we have : $\mu_1 = \mu_v(t_v,\mu_2)$ (9),
170 where t_v denotes the duration of the current vigilant interval.

171 **Updating the perception of the overall level of environmental risk**

172 Here, we explore the possibility that the observations made by the forager in its immediate
173 neighbourhood also convey information about the likelihood of the predator's presence in the
174 surrounding places. Thus, we study the process whereby, if the predator, which is mobile, has
175 not been detected for a certain period of time in the neighbourhood, it becomes more likely
176 that it is indeed absent from the whole environment.

177 In the model, this means that parameter P_0, which estimates the probability of the
178 predator's presence in the whole environment, also becomes the object of an updating process.
179 We assume that this updating process takes place at the end of each scanning interval. P_n
180 denotes the estimated probability of the predator's presence in the whole environment
181 immediately after scan n, still conditional on the absence of any detection. $Q(t_v,P_n)$ denotes
182 the probability that the predator is present in the environment, but remains undetected during
183 a scanning interval of duration t_v, when the probability of the predator's presence in the
184 environment is P_n (see Appendix A). Using Bayes formula, we have :

185 $$P_{n+1} = Q(t_v,P_n)/(Q(t_v,P_n) + 1 \times (1-P_n)) \quad (10).$$

186 Eq. (10) is used to update the value of P at the end of each scanning interval. The
187 dynamics of risk perception during the following interscan and scan is then computed using
188 Eqs. (4) and (8), respectively, with this updated value.

189 The situation where parameter P is the object of an updating process yields relatively
190 complex vigilance behaviour, with scans and interscans that progressively vary in duration
191 (see Results). In the following section, which is dedicated to the influence of ecological
192 parameters on vigilance strategies, we do not consider this effect of time. P_0 is thus treated as
193 a constant.

194

195

196 **Optimal vigilance**

197 Here we define a fitness measure which takes into account the advantages of vigilance, in
198 terms of reduced exposure to the predator, and its drawbacks, in terms of lost feeding time. In
199 the framework of a constantly fluctuating level of perceived risk, the vigilance strategy of the
200 forager is associated with the range of tolerated risk levels, $[\mu_1,\mu_2]$. The analysis of risk
201 perception dynamics presented above shows that, when μ_1 is not too low and μ_2 not too high
202 (i.e. $\mu_1 > a$ and $\mu_2 < \mu_0$), we can find one single set of durations for scans and interscans,
203 hereafter denoted by t_v and t_f, respectively, for which the level of risk perceived by the forager
204 describes interval $[\mu_1,\mu_2]$ during each scan/interscan cycle. These durations verify Eqs. (5)
205 and (9). The range of risk levels tolerated by the forager thus induces a single vigilance
206 strategy, characterized by feeding and vigilant intervals of constant durations.

207 We assume that the forager always escapes if it detects the predator while vigilant. In
208 this situation, the total time lost in the current scan and in the escape, T_E, only impedes its
209 overall feeding rate. The probability that the predator is detected during a scan is : $P_D = P_0 -$
210 $Q(t_v,P_0)$, since $Q(t_v,P_0)$ is the probability that the predator is present in the environment, but
211 remains undetected during the scan (see Appendix A).

212 For the forager, the total level of exposure to predation risk thus only depends on the
213 number and duration of feeding periods, and on the probabilities of the predator's presence
214 during these periods. This simplifying assumption conserves the advantages of vigilance,
215 namely, the fact that the forager has more chance of escape if attacked while vigilant than
216 while feeding, and the fact that it endures a reduced level of risk when returning to feed after
217 a vigilant period during which no detection occurred.

218 We consider a given feeding period. t denotes the time elapsed since the forager
219 resumed feeding, and $P_{NE}(t,\mu_1)$ is the probability that the forager has not been exposed to the
220 predator at time t. We make the per time unit probability of exposure to predation risk equal

to the estimated probability of the predator's presence. Since $\mu_f(t,\mu_1)$ is the probability of the predator's presence in the neighbourhood at time t, we have :

$$P_{NE}(t+dt,\mu_1) = P_{NE}(t,\mu_1) \times (1-\mu_f(t,\mu_1)dt) \quad (11),$$

which leads to the differential equation : $dP_{NE}/dt \times 1/P_{NE} = - (\mu_1-\mu_0) \times \exp(-mxt) - \mu_0$ (12).

The solution of Eq. (12) is : $P_{NE}(t,\mu_1) = \exp(-\mu_0 xt) \times \exp((\mu_1-\mu_0) \times (\exp(-mxt)-1) / m)$ (13).

Hence, the probability of not being exposed to the predator's presence during a feeding period of duration t_f is $P_{NE}(t_f,\mu_1)$, and the probability of not being exposed to the predator's presence during the whole foraging bout is $P(t_f,t_v) = (P_{NE}(t_f,\mu_1))^n$, where $n = T/(t_f + (1-P_D)xt_v+P_D \times T_E)$ is the total number of feeding periods.

The expected energy gain for the whole foraging bout, provided the individual survives, is : $E(t_f,t_v) = n \times (t_f \times g - e)$, where g is the energy gain per time unit of feeding, and e the energy cost of switching from vigilance to feeding, then from vigilance to feeding.

To compute optimal strategies in a way that takes into account both the advantages and the drawbacks of vigilance, we use the following quantity to measure fitness :

$$F(t_f,t_v) = P(t_f,t_v) \times E(t_f,t_v) \quad (14).$$

The individual does indeed increase its probability of not being exposed to the predator, $P(t_f,t_v)$, by being more vigilant, but, at the same time, it reduces its energy gain $E(t_f,t_v)$. Fitness as defined by Eq. (14) thus allows to study the response to the trade-off between feeding and limiting exposure to predators (see Packer and Abrams, 1990; Brown, 1999). The optimal vigilance strategy is the set of values (t_f,t_v) for which $F(t_f,t_v)$ is maximized. It is derived numerically.

RESULTS

Fluctuations of risk perception

After a relatively long initial scan following the arrival on the patch, the level of risk perceived by the animal begins to fluctuate in a periodic way. It increases during each interscan, then decreases again during the following scan, with dynamics respectively given by Eqs. (4) and (8) (Fig 1). Excepted for the long initial scan, both scans and interscans have constant durations, which depend on this dynamics and on the range of risk levels $[\mu_1,\mu_2]$ tolerated by the forager.

Compared to a control situation (dashed line, $t_v = 5.99$, $t_f = 5.03$), the detection capacity of the forager is increased by increasing the value of parameter D, which measures this capacity (full line). As a consequence, the level of risk perceived decreases faster during scans, while the dynamics of risk perception does not change during interscans. To maintain the level of risk perceived within the same interval, the forager thus shortens its scans, while the duration of interscans remains the same (full line, $t_v = 2.14$, $t_f = 5.03$). By contrast, if the level of danger is decreased by reducing the overall likelihood of the predator's presence in the environment (i.e. parameter P_0, dotted line), the dynamics of risk perception is affected during both scans and interscans, because the arrival of the predator becomes less likely during both kinds of intervals. The level of risk perceived thus decreases more rapidly during scans, and increases more slowly during interscans (compare dotted and dashed line). The forager thus responds to this situation by shortening its scans, and increasing its interscans (dotted line, $t_v = 3.5$, $t_f = 8.11$). Qualitatively similar results are obtained when the level of danger is increased by an increased mobility of the predator (data not shown).

Updating the perception of the overall level of environmental risk

Here we explore the situation where the observations made by the forager in its immediate neighbourhood contribute to update its estimate of the probability of the predator's presence in the whole environment.

The effect of this updating process is that, over a foraging bout during which the predator is not detected, the estimated probability of the predator's presence in the whole environment (i.e. P) progressively decreases with time. As a consequence of this declining perception of the overall level of risk, the level of risk perceived locally decreases more rapidly during scans, and increases less rapidly during interscans, as predicted when the value of P_0 is decreased (see Fig 1). The proportion of time dedicated to vigilance thus progressively declines (see Fig 2).

Logically, additional simulations show that when s/S, the proportion of the whole environment that is observable by the forager, gets smaller, vigilance decreases more slowly.

Optimal vigilance

Here we study how the optimal vigilance strategy varies with ecological conditions. The level of environmental danger increases when either the likelihood of the predator's presence in the whole environment, P_0, or its mobility, m, increases (Fig 3a,b), and when the detection ability of the forager, D, decreases (Fig 3c).

In the three situations, the durations of both scans and interscans change as a response to an increased level of danger, and the proportion of time dedicated to vigilance increases. The effects of increasing the likelihood of the predator's presence in the environment, or the mobility of the predator, are similar. In both cases, scans get longer, and interscans shorter (Fig. 3a,b). By contrast, when the level of exposure increases because the detection capacities of the prey are reduced, the increase in vigilance only results from the lengthening of scans, which, as they become longer, also become separated by longer feeding intervals (Fig 3c).

DISCUSSION

In the present article, we study how the alternation of anti-predatory vigilance and feeding intervals determines the levels of risk successively perceived by a forager, in an environment potentially occupied by a predator. The model dedicates special attention to the process of information acquisition during scans, as information gathering is the primary function of vigilance, and considers the loss of this information during feeding intervals.

In the first part of the study, we compute the dynamics of predation risk perception, in the common situation where no detection occurs. We show how the level of risk perceived continuously vary with the activity of the animal, decreasing during scans, as the animal accumulates information about safety in the environment, then increasing again during interscans, when it is no longer able to detect the possible arrival of the predator. The speed of these variations, combined with the range of risk levels tolerated by the animal, finally determines its vigilance strategy, which means that the range of risk levels accepted by the forager and its vigilance behaviour are both tightly connected to the dynamics of risk perception. The model shows that this dynamics should tend to make the duration of both scans and interscans relatively constant. However, the initial scan should always be longer than the following ones, and, if we take into account the possibility for the forager to learn about surrounding places through its local observations, the proportion of time dedicated to vigilance should decline with time. Such progressive decrease in vigilance following the arrival into a novel environment has been reported in harbour seals, *Phoca vitulina*, attending haul out sites (Terhune and Brillant, 1996).

In real conditions, however, the regular dynamics of predation risk perception predicted by our model will be disturbed by accidental changes, coming from external events (such as unidentified shapes or noises; Ruxton and Roberts 1999), or observation of companions, whose behaviour may convey information about potential predators (Fernández

et al., 2003), and influence individual predation risk in several ways (Sirot and Touzalin, 2009). As a consequence, the individual will reach the critical switching values for predation risk perception at different moments, which will induce some variability in the temporal patterns of vigilance (see Ruxton and Roberts, 1999).

Nevertheless, the mechanism described here, whereby predation risk perception progressively increases during interscans, until it triggers a switch to vigilance, and progressively decreases during vigilance, until the level of safety allows the animal to resume feeding, should contribute to reduce the variability of the duration of both scans and interscans, and the instantaneous probability of switching should increase with time, during both kinds of intervals. The model thus proposes an alternative, based on mechanistic and adaptive reasoning, to the original hypothesis of vigilance studies that scans should be initiated with a constant rate (that is, with a constant per time unit probability; Pulliam, 1973). In accordance with our results, several studies demonstrate that the per time unit probability of looking up increases as an animal feeds, instead of being constant (Hart and Lendrem, 1984; Sullivan, 1985; Lendrem et al., 1986; Beauchamp, 2006; Pays et al., 2010). As a consequence, both short and long interscans become more rare than under the original hypothesis of a constant scan initiation rate. Scan duration has received much less attention than interscan duration (Bednekoff and Lima, 1998). The present model suggests that it should also be relatively constant. The fact that the efficiency of vigilance declines with time, because attention cannot be sustained for long periods, should reinforce this tendency (Dukas and Clark, 1995).

In the second part of the study, we derive optimal strategies for the alternation of scanning and interscan intervals. Doing so, we make several simplifying assumptions. First, we assume that a feeding individual cannot detect predators, whereas an animal may retain limited detection capacities when it searches for food (Lima and Bednekoff, 1999). However,

even animals with such ability also possess characteristic vigilance attitudes, with erect postures of the neck or the whole body (Bednekoff and Lima, 2005; Ebensperger and Hurtado, 2005). This situation could thus be studied under the present framework. Including a limited detection ability for feeding individuals would quantitatively affect the results of the model, by slowing the resilience of risk estimation during interscans, but not its general qualitative predictions. Reciprocally, overtly vigilant individuals may sometimes continue to feed. For example, birds swallowing seeds raise their heads, which allows them to scan (Baker et al., 2010), and large herbivores may also become vigilant while chewing (Fortin et al., 2004). In these conditions, feeding does only partially, or not at all, impede vigilance, and the temporal pattern of vigilance is dependent on the feeding method. We can hypothesize that this process should contribute to make interscans more variable in length, as the time necessary to gather food on the ground is variable, and scans more constant, as the handling time for one particular type of food should be relatively constant.

Second we chose, for the sake of mathematical tractability, to consider the probability of the predator's presence as a measure of risk, thus assuming that minimizing predation risk is equivalent to limiting exposure to the predator's presence. In reality, predation risk also depends on the behaviour of the predator, which could in principle adapt its hunting behaviour to the vigilance displayed by the prey, thus initiating a game between predator and prey. The outcome of such a game on temporal patterns of prey vigilance has been studied by Scannell et al. (2001) and Bednekoff and Lima (2002), who identified two situations. In the first one, predators are prevented from timing their attack according to the vigilance schedule of the prey, for example because they have to cross a large portion of open space when attacking. In this situation, scanning at regular intervals is an advantage. By contrast, scanning at irregular intervals could be the best strategy against stalking predators that launch their attacks from close distances (Scannell et al., 2001; Bednekoff and Lima, 2002). The

mechanism described in the present study could thus, in some situations, be reinforced by the necessity to counter the hunting strategy of the predator. In others, the prey should simultaneously compromise with an efficient handling of the information garnered through vigilance, and an appropriate response to the tactic of the predator.

The levels of risk accepted by an animal are also expected to depend on the level of its energy reserves, which may fluctuate in a non-deterministic way. For example, an animal may be prevented from feeding for a part of the day. It will thus have low levels of reserves, and should become relatively risk tolerant, especially if the end of the foraging period is getting near (McNamara and Houston, 1986). Reciprocally, an animal with important levels of reserves could afford to invest more in anti-predatory vigilance (Beale and Monaghan, 2004). Across a foraging bout, the variations of individual levels of reserves and the Bayesian updating process concerning the prevailing level of risk could thus have conflicting effects on the level of vigilance. A model incorporating both a state-dependent approach and a description of the dynamics of risk perception should allow to study how the range of tolerated levels of risk could vary, according to current level of reserves of the animals and the time of the day.

In accordance with other models (e.g. McNamara and Houston, 1992; Brown, 1999), our model predicts higher vigilance in dangerous environments. This increase in vigilance is achieved by longer and more frequent scans when the likelihood of the predator's presence in the environment is high, and when the predator is highly mobile. By contrast, scan should increase in length, but not in frequency, when danger originates from decreased detection capacities for the prey. Additional simulations show that, when the cost of switching e is reduced and tends towards zero, the durations of both scans and interscans also tend towards zero, while the proportion of time spent vigilant does not change. Thus, we can draw the prediction that an animal will prefer to alternate between feeding and vigilance at the

maximum rate that is compatible with the efficiency of both feeding and vigilance activities. In this way, it will avoid sporadic periods of high risks, corresponding to high values of μ_2.

Field studies confirm that vigilance rises during periods of increased predator activity (e.g. Caraco et al. 1980; Scheel, 1993; Devereux et al., 2005). Vigilance is often measured as the proportion of time spent vigilant, but the effects of environmental conditions on scan and/or interscan lengths have also been considered in several studies. The level of risk endured by the animals generally corresponds to the amount of obstructive cover near the feeding place, which hinders predator detection (Harkin et al., 2000). In accordance with the predictions of the model, the proportion of time spent vigilant generally increases with the proximity of obstructive cover (e.g. Underwood, 1982; Lazarus and Symonds, 1992; Watson et al., 2007; but see Scheel, 1993), and scanning intervals become longer (Metcalfe, 1984; Goldsmith, 1990; Pöysä, 1994). Interestingly, scans may become more frequent when they get longer (McVean and Haddlesey, 1980; Metcalfe, 1984; Goldsmith, 1990), but this is not always the case (Pöysä, 1994; Whittingham et al., 2004). Reciprocally, increases in scanning rate with no concomitant changes of scan duration have also been reported, although these results concern circumstances that are not considered in the present study (in Lendrem's (1983) study on house sparrows *Passer domesticus*, an individual could leave its feeding place to join a better observatory, and in Bertram's (1980) study on ostriches *Struthio camelus*, the increased level of vigilance was a response to a smaller group size). Thus, field studies show that the duration and frequency of scanning intervals may not always vary together, and tracking the variations of individual perception of predation risk may provide the key to understanding these patterns. As an extension of the present model, it would be interesting to consider how individual perception of risk is modified by the presence and behaviour of companions in a group, thus using the individual-based approach presented here to study the role played by social information in collective vigilance.

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Appendix A. Probability of not detecting the predator during a scanning interval.

Here we compute $Q(t_v,P_n)$, the probability of not detecting the predator during a scanning interval of duration t_v, when the probability of the predator's presence in the whole environment is P_n. Two cases must be considered.

First, the predator may initially be present in the neighbourhood of the forager. This happens with probability μ_1, which corresponds to the level of risk perceived at the end of the vigilant interval. At time t, the predator is still present and has remained undetected with probability $\exp(-(m+D)\times t)$, since both movements and detection are Poisson processes. If still present, the predator will be detected during small interval dt with probability Ddt. Thus, the probability of not detecting the predator over the whole scanning interval of duration t_v when it is initially present in the neighbourhood, is :

$$Q_1(t_v) = 1 - \int_0^{t_v} [\exp(-(m+D)\times t)\times D]dt = m/(m+D) + D/(D+m) \times \exp(-(D+m)\times t_v) \qquad (A1).$$

Second, the predator may initially be present in the environment, but not in the neighbourhood of the forager. This happens with probability $P_n - \mu_1$. The arrival of the predator in the neighbourhood of the forager is then a Poisson process of parameter $m' = m\times s/S$. The probability that the predator arrives between time t and t + dt is thus $\exp(-m'\times t)\times m'dt$, and the probability that it is detected before the end of the scan, that is, during the time that remains, is given by : $1 - Q_1(t_v-t)$ (see Eq. (A1)). Thus, the probability of not detecting the predator if it is initially present in the environment, but not in the neighbourhood of the forager, is :

441 $$Q_2(t_v) = 1 - \int_0^{t_v} [\exp(-(m' \times t)) \times m' \times (1 - Q_1(t_v - t))]\, dt \quad \text{(A2)},$$

442 which leads to :

443 $Q_2(t_v) = 1 - m' \times D/(m+D) \times ((1-\exp(-m' \times t_v))/m' - 1/(D+m-m') \times (\exp(-m' \times t_v) - \exp(-(D+m) \times t_v)))$ (A3).

444 We finally have : $Q(t_v, P_n) = Q_1(t_v) \times \mu_1 + Q_2(t_v) \times (P_n - \mu_1)$ (A4).

445

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LEGENDS

Fig. 1

Fluctuations of risk perception during successive scanning and interscan intervals for a foraging bout during which no detection occurs. The dynamics for the estimated probability of the predator's presence in the neighbourhood are given by Eqs. (4) and (8) for interscans and scans, respectively. Parameter values : $[\mu_1,\mu_2]$ = [0.01,0.03], s/S = 0.1, dashed line : P_0 = 1, m = 0.05, D = 0.5, full line : P_0 = 1, m = 0.05, D = 0.8, dotted line : P_0 = 0.7, m = 0.05, D = 0.5.

Fig. 2

Fluctuations of risk perception during successive scanning and interscan intervals for a foraging bout during which no detection occurs, when the estimated probability of the predator's presence in the whole environment is updated after each scanning interval. The graph also shows, for each scan/interscan cycle, the proportion of time dedicated to vigilance (full line). Parameter values : $[\mu_1,\mu_2]$ = [0.01,0.03], P_0 = 0.8, s/S = 0.1, m = 0.07, D = 0.5.

Fig. 3

Optimal vigilance strategy, represented by the values of t_f (length of feeding periods), t_v (length of vigilance periods after the initial scan), and u (proportion of time dedicated to vigilance), as a function of an increasing likelihood of the predator's presence in the whole environment (panel (a)), an increasing mobility of the predator (panel (b)), and a decreasing detection ability for the forager (panel (c)). Parameter values : g = 1, e = 0.001, T = 100, s/S = 0.1, (a) m = 0.05, D = 0.5, (b) D = 0.5, P_0 = 1, (c) m = 0.05, P_0 = 1.

Fig. 1

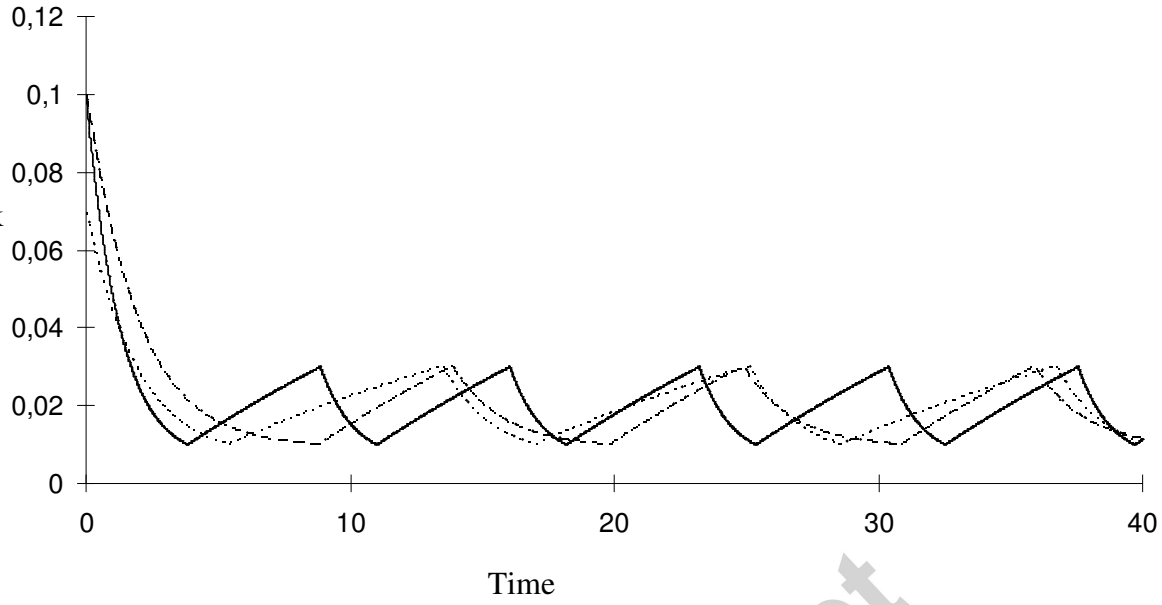


Fig. 2

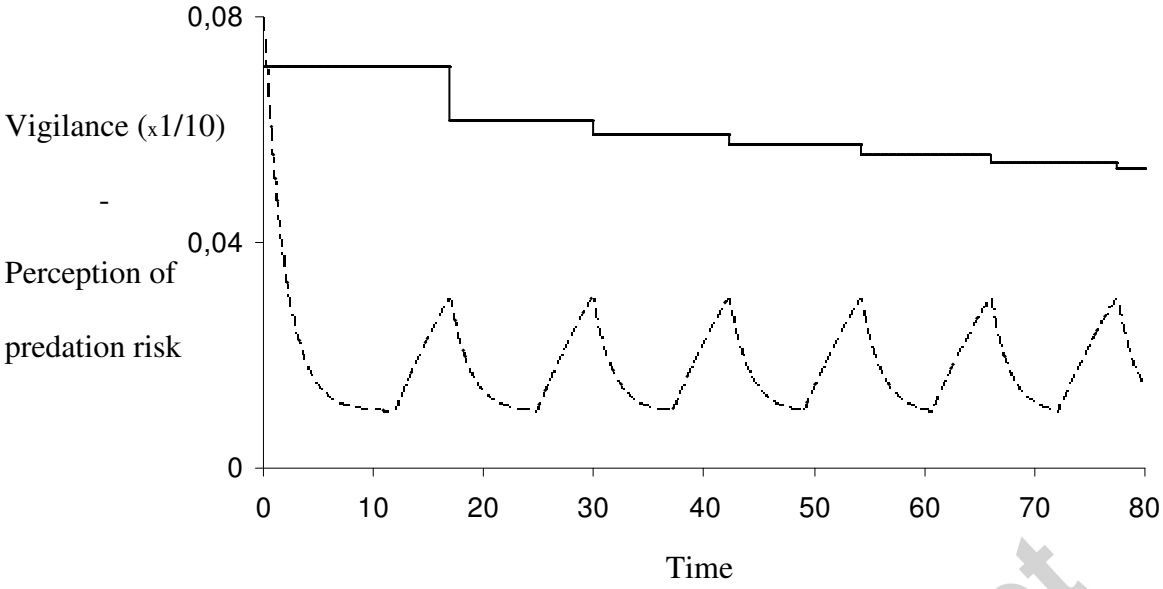
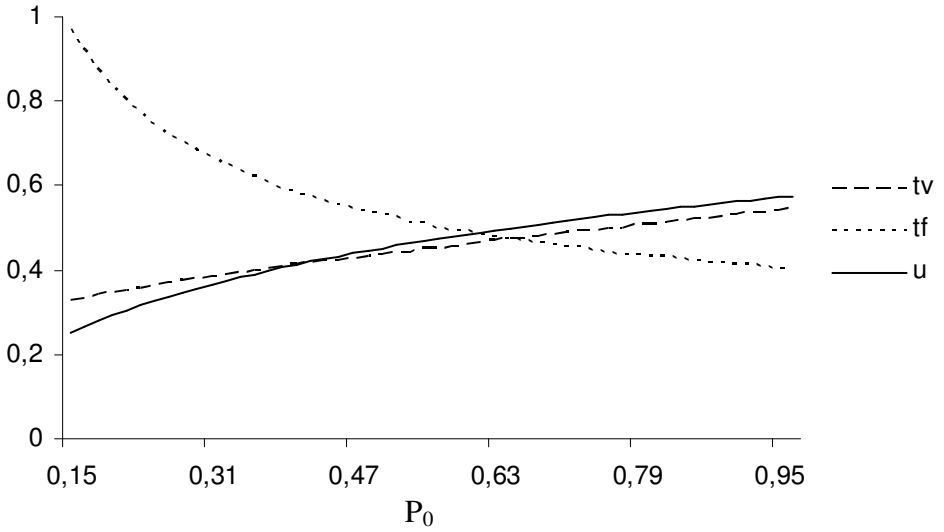


Fig. 3 (a)



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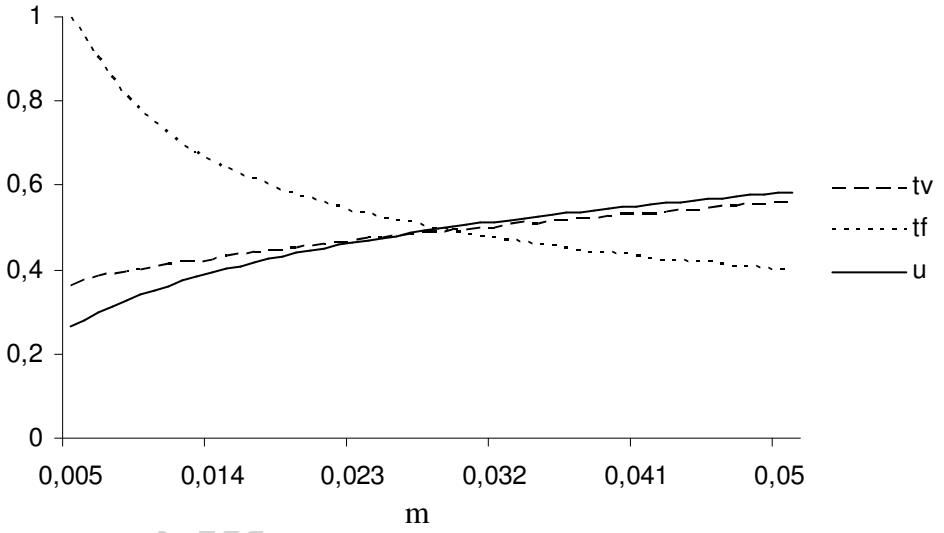

(c)